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16. ABSTRACT

The behavioral responses of fishes, specifically preference and avoidance reactions, to temperature are described using a general graphical model based on a broad overview of the literature. A quantitative measure of eurythermality, based on the area of the thermal preference zone, is presented which offers a more meaningful estimate of the optimal thermal requirements of the species than one based on lethality alone. We also emphasize the importance of considering the preference-avoidance responses of fishes when setting ambient water quality criteria for temperature or when estimating the potential environmental impact resulting from changes in the thermal regime of an aquatic system.

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# Graphical Model of Thermoregulatory Behavior by Fishes with a New Measure of Eurythermality

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The behavioral responses of fishes, specifically preference and avoidance reactions, to temperature are described using a general graphical model based on a broad overview of the literature. A quantitative measure of eurythermality, based on the area of the thermal preference zone, is presented which offers a more meaningful estimate of the optimal thermal requirements of the species than one based on lethality alone. We also emphasize the importance of considering the preference–avoidance responses of fishes when setting ambient water quality criteria for temperature or when estimating the potential environmental impact resulting from changes in the thermal regime of an aquatic system.

*Key words*: thermoregulation, behavior, temperature, eurythermality, thermal preference, avoidance

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Un modèle graphique général fondé sur un survol des travaux publiés sert à décrire les réponses éthologiques des poissons, particulièrement les réactions de préférence et d'évitement de la température. Nous donnons une mesure quantitative de l'eurythermalité, fondée sur la superficie de la zone de préférence thermique. Cette mesure conduit à une meilleure estimation des exigences thermiques optimales de l'espèce qu'une estimation fondée sur la létalité seule. Nous faisons en outre ressortir l'importance de tenir compte des réponses de préférence–évitement des poissons en établissant les critères de qualité de l'eau ambiante quand à la température ou en estimant l'impact environnemental qui pourrait résulter de changements dans le régime thermique d'un système aquatique.

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FOUR general hypotheses have emerged as unifying concepts in the study of behavioral thermoregulation by fishes: (1) the final temperature preferendum is a species-specific response to a temperature gradient, but can be modified by nonthermal acclimatization factors, such as age, food availability, season, or pathologic condition (e.g. Sullivan and Fisher 1953; McCauley and Read 1973; Peterson 1973, 1976; Reynolds and Casterlin 1976, 1978a, 1980; Reynolds et al. 1976; McCauley 1977); (2) habitat partitioning by thermoregulatory behavior is one means of segregating fishes both intra- and inter-specifically, thereby reducing cannibalism and competition (e.g. Reynolds and Casterlin 1978b; Brandt et al. 1980; Coutant 1980; Crowder et al. 1981); (3) preferred temperatures may reflect thermal optima for certain biological processes (e.g. Crawshaw 1977; Magnuson et al. 1979; Coutant 1980); and (4) fishes generally avoid thermal extremes before they become lethal, provided favorable temperatures (thermal refugia) are available (e.g. Cherry et al.

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1975, 1977; Gift 1977; Winkler 1979). The *sine qua non* of each hypothesis is the ability of fishes to perceive and to respond to temperature changes in an adaptive manner. After we conducted a broad review of the literature, it became apparent that the behavioral responses of fishes (preference and avoidance) to temperature could be summarized with a general graphical model which provides a conceptual framework for understanding the more elusive effects temperature has on the movements of many fish species. The purpose of this paper is to present this model with supporting data from the literature, and to define (using the model) a quantitative measure of eurythermality based on behavioral responses to temperature.

*Definition of terms* — A variety of laboratory methods have been used to determine the thermal responses of fishes (McCauley 1977). In general, regardless of the methods used, laboratory studies have demonstrated the abilities of fishes to thermoregulate behaviorally within relatively narrow limits. A measure of the central tendency (mean, mode, median, or midpoint) of the frequency distribution of a fish species within a laboratory thermal gradient over a short period of time (2 h or less) is termed the *acute preferred* or *acute thermal preferendum* (Reynolds and Casterlin 1979a), which is highly dependent on acclimation temperature (see Mathur and Silver (1980) for discussion of statistical problems associated with acute temperature preference studies). The *final temperature preferendum*, on the other hand, is the temperature around which fish finally will congregate given the opportunity to do so in a thermal gradient of sufficient extent (Fry 1947). This value is independent of acclimation temperature and can either be measured directly over a period of 1–4 d (Richards et al. 1977), or estimated as the temperature at which the preferred temperature equals the acclimation temperature. When placed in a gradient, fish acclimated to temperatures below their final preferendum will generally move into higher temperatures (acute thermal preference), resulting in a progressive and relatively rapid increase in acclimation temperature for the fish. This upward trend in temperature preference occurs until the final preferendum is attained, and the fish continues to thermoregulate around this temperature. If the gradient is spatially shifted, fish will move with the gradient so that body temperatures are maintained within narrow limits ("isotherm-tracking" (Reynolds and Thomson 1974; McCauley et al. 1977)).

Avoidance responses of fishes to temperature also have been determined using a variety of techniques. Generally, avoidance can be measured directly by providing fish with a choice between water which is heated or cooled and water at the acclimation temperature of the fish (e.g. Meldrim and Gift 1971 and Cherry et al. 1975, 1977, as modified from Shelford and Allee 1913). The avoidance threshold, then, is defined as the temperature at which fish spend significantly less time in comparison to controls. Avoidance can also be estimated indirectly by determining the median upper and lower turnaround temperatures using an electronic shuttlebox (Neill et al. 1972; Neill and Magnuson 1974); turnaround temperatures are defined as the local temperature maxima and local temperature minima recorded from the warmer and cooler sides of the tank, respectively (Neill and Magnuson 1974).

Although the words "selection" and "preference" have been used synonymously in the literature, "selection" might be mistaken for "natural selection" as an evolutionary process. For this reason, we prefer the term temperature preference in the organismic context.

*Model of thermoregulatory behavior* — Temperature preference and temperature avoidance are simply opposite sides of the same coin (Reynolds 1977); these responses are inseparable aspects of behavioral thermoregulation under natural conditions. Given this, it is not surprising to find that both preference and avoidance behavior are altered by a variety of environmental, as well as anthropogenic, factors. Preference–avoidance responses to temperature can vary on a diel and/or seasonal basis which may reflect changing thermal requirements for a species over time (Sullivan and Fisher 1953; McCormick et al. 1977; Reynolds and Casterlin 1979b, 1980). Also, changes in water quality, light intensity, food availability, competition, bacterial infections, and age can alter the thermoregulatory behavior of any given species under laboratory conditions (Sullivan and Fisher 1954; Ferguson 1958; Ogilvie and Anderson 1965; Covert and Reynolds 1977; Reynolds et al. 1977; Coutant 1980). Despite the many complicating factors that are possible, comprehensive field investigations have shown that temperature is extremely important in determining the distribution patterns of many species, and these patterns can be predicted on the basis of temperature preferenda of the individual species (Neill and Magnuson 1974; Stauffer et al. 1976; Coutant 1980). In addition, avoidance responses under field conditions have been documented by many authors for a variety of species (e.g. McCauley and Tait 1970; Marcy et al. 1971; Cherry et al. 1976; Ehrlich et al. 1978; Winkler 1979). Overwhelming evidence, therefore, supports the general conclusion that the preference–avoidance response to temperature is an ecologically significant behavior that influences the distributions and movements of fishes. Variability of this behavior under different sets of conditions is not unusual, considering that habitat selection is based on the optimization of various environmental factors which fit the particular morphological, physiological, and behavioral characteristics of a species. Thus, the relative influence of each environmental factor on thermoregulatory behavior in a natural ecosystem will most likely change depending upon the biological "needs" of an organism at a particular time.

Before any reliable recommendations can be made concerning appropriate water quality criteria for temperature, and before reliable estimates of the potential impact of thermal discharges on aquatic resources can be made, behavioral responses of indigenous species must be considered (Hoss et al. 1979). The behavioral model we propose offers a general means of viewing the sublethal effects of temperature on locomotor behavior in relation to lethal effects (Fig. 1). This model is patterned after the classical temperature tolerance polygon described by Fry (1947) and Brett (1956), and was suggested from data presented by Reynolds and Casterlin (1979a) on the thermal relations of bluegill sunfish (*Lepomis macrochirus*). The thermal tolerance polygon was based on the incipient lethal temperature, defined as that temperature beyond which 50% of the population could no longer live given an indefinite period of time (Fry 1947). Fishes, however, are more sensitive to thermal changes than direct lethal

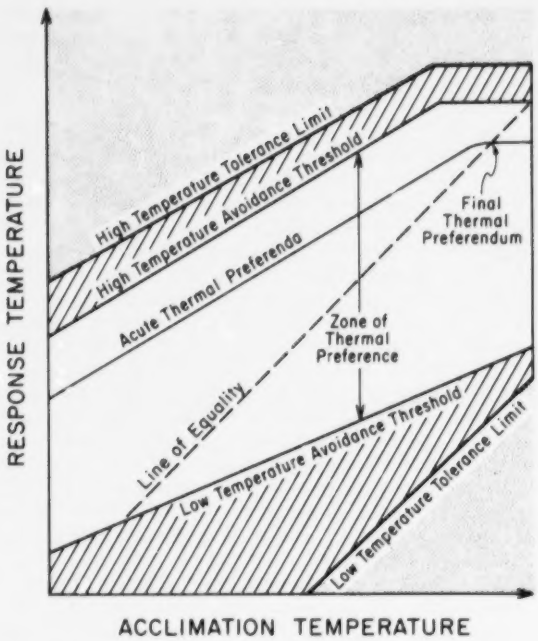


FIG. 1. Generalized graphical model which demonstrates the relationships between preferred, avoided, and lethal temperatures. Broken line (line of equality) represents points at which preferred temperature equals acclimation temperature, and is often used in estimating the final thermal preferendum.

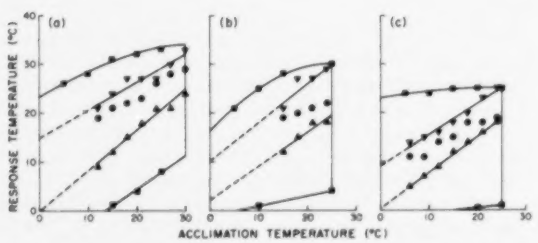


FIG. 2. Acute thermal preferenda (●), upper (▼) and lower (▲) avoidance temperatures, and lethal temperatures (■) for (a) bluntnose minnow (*Pimephales notatus*), (b) yellow perch (*Perca flavescens*), and (c) brook trout (*Salvelinus fontinalis*). Lethal temperatures were reported by Brett (1956); avoidance and acute thermal preferenda were reported by Cherry et al. (1975, 1977).

effects generally indicate. Given the choice, many species will avoid temperatures below the incipient lethal level; therefore, based on the previous discussion, it is apparent that a more detailed conceptual framework is needed to assess fish responses to temperature changes. This framework is provided in Fig. 1. The avoidance temperatures are within the range of nonlethal temperatures and bound an area referred to as the zone of thermal preference. Within this area, the acute thermal preferenda and the final thermal preferendum are distributed asymmetrically, falling closer to the upper zone of lethality. This reflects the observation that many fish prefer, without apparent harmful effects, temperatures only a few degrees below those that are lethal. The data reported for a variety of fish species are consistent with this graphical model (Fig. 2; see also Reynolds and Casterlin 1979a, 1980).

By measuring the area within the temperature tolerance polygon, Brett (1956) gave a numerical estimate (expressed as $°C^2$) of the range of thermal conditions an organism could withstand. Perhaps a better quantitative estimate of the optimal thermal requirements of an organism, however, is provided by the area within the temperature preference zone. This would also represent a more realistic quantitative measure of the qualitative terms "eurythermal" and "stenothermal," as suggested by Cherry et al. (1975). For example, the zones of tolerance for bluntnose minnow (*Pimephales notatus*), yellow perch (*Perca flavescens*), and brook trout (*Salvelinus fontinalis*) were calculated to cover areas of 808, 742, and $625°C^2$ (thermal tolerance units), respectively (Brett 1956). The zones of thermal preference for each species, however, are considerably more limited, covering areas of 338, 239, and $186°C^2$ (thermal preference units), respectively. The importance of this zone of thermal preference lies in the third hypothesis presented above, i.e. preferred temperatures may reflect thermal optima for certain biological processes. Fishes, because of their species-specific temperature preferences, segregate along thermal gradients (thermal partitioning: Reynolds and Casterlin 1978b; Brandt et al. 1980; Coutant 1980; Crowder et al. 1981). Given this, one logical assumption would be that biological processes, although capable of functioning over the range of normal habitat temperatures for a species, would function best at or near the temperature preferred by that species (e.g. Crawshaw 1977; Magnuson et al. 1979; Coutant 1980). If, then, fishes actively select temperatures that are optimum for meeting their biological needs at a particular time (certainly some evidence indicates that they do), then the zone of thermal preference, as presented in our model, may be a more accurate representation of the thermal regime a species will inhabit.

Thus, because of behavioral effects, the sublethal environmental impacts of temperature on fish communities are more subtle, but potentially as drastic as direct lethality. For example, under late fall or early spring conditions, assuming an acclimation temperature of about 10°C, brook trout prefer temperatures within the avoidance limits of 7–16°C (Fig. 2). According to our model, a water temperature greater than 16°C would have caused brook trout to avoid the area of thermal impact, even though they could have tolerated temperatures up to 24°C for some period of time.

Temperature changes could be caused by industrial thermal inputs or by unnatural heating of an aquatic system due to deforestation, impoundment, or other changes in the watershed. These changes may be undesirable in that they reduce the area of the stream having temperatures within the zone of thermal preference, and thus reduce desirable habitat for fish species. Thus, one factor affecting the severity of any thermal impact on a fish community is the area or volume of the aquatic environment affected. If the undesirable temperature effectively blocked migratory routes of passage (in lotic systems), or rendered large areas of the habitat unavailable for reproduction or feeding (in lentic systems), then the potential loss to a species would be greater than that estimated on the basis of lethality alone. Conversely, if the area of impact

were relatively small, with suitable areas of refuge or routes of passage left open, then the thermal impact would be minimal for many fish species. The potential impact of any thermal change, therefore, will be governed to a great extent by the site-specific physical characteristics of the aquatic system affected.

The graphical model we present (Fig. 1) provides a general scheme for understanding the sublethal effects temperature has on the movements of many fish species, and a more meaningful interpretation of eurythermality. Of primary importance, however, is the additional understanding gained from considering behavioral effects. By doing this, environmental scientists and managers will have a broader perspective for predicting the consequences of thermal changes in aquatic systems.

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